Geophysical Research Letters

Ocean Acidification Has Impacted Coral Growth on the Great Barrier Reef

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Abstract Ocean acidification (OA) reduces the concentration of seawater carbonate ions that stony corals need to produce their calcium carbonate skeletons and is considered a significant threat to the functional integrity of coral reef ecosystems. However, detection and attribution of OA impact on corals in nature are confounded by concurrent environmental changes, including ocean warming. Here we use a numerical model to isolate the effects of OA and temperature and show that OA alone has caused $13 \pm 3\%$ decline in the skeletal density of massive *Porites* corals on the Great Barrier Reef since 1950. This OA-induced thinning of coral skeletons, also evident in *Porites* from the South China Sea but not in the central Pacific, reflects enhanced acidification of reef water relative to the surrounding open ocean. Our finding reinforces concerns that even corals that might survive multiple heatwaves are structurally weakened and increasingly vulnerable to the compounding effects of climate change

Plain Language Summary Measurable anthropogenic-induced acidification of the oceans (OA) has occurred over the last four decades. But its impact on coral reef ecosystems, such as coral calcification, has yet to be unambiguously demonstrated. This problem with detection and attribution of OA impacts is due, in large part, to the fact that multiple co-varying environmental and biological factors influence coral growth at the same time, and our inability to deconvolve them. Here, we use a numerical model of coral growth to isolate the contributions of ocean acidification to long coral growth timeseries generated on multiple Indo-Pacific reefs over the 20th century. We show that ocean acidification has had a significant negative impact on skeletal growth of a keystone reef-building genus across the Great Barrier Reef and in the South China Sea, where the rate of reef acidification outpaces that of the surrounding open ocean. Conversely, the OA-induced thinning of coral skeletons observed on these reefs has not yet affected corals in the central Pacific, where the rates of reef acidification have been lower. Nevertheless, as ocean acidification accelerates over the next few decades, even these reefs will be affected, resulting in a measurable weakening of coral reef structures across the global tropics.

1. Introduction

About one third of the CO_2 emitted to the atmosphere by human activities has been absorbed by the oceans, driving about 0.1 unit decline in ocean pH and a corresponding ~20% decrease in carbonate ion concentration ($[CO_3^{2-}]$) since the preindustrial era (e.g., Doney et al., 2009; Feely et al., 2009; Friedlingstein et al., 2019). This process, known as ocean acidification (OA), is expected to continue through this century and beyond, causing another 0.1–0.4 unit pH decline by 2100 and effectively halving the concentration of carbonate ions in seawater relative to the preindustrial era (e.g., Doney et al., 2009; Feely et al., 2009; Orr et al., 2005). Calcifying organisms, which need carbonate ions to form their skeletons, are most at risk, and coral reef ecosystems are expected to be heavily impacted (e.g., Hoegh-Guldberg et al., 2007; Orr et al., 2005). Laboratory experiments that reared corals and other coral reef calcifiers under high CO_2 conditions, as well as field studies of naturally low-pH reefs, indicate, in general, that decreased rates of calcification and increased rates of dissolution and bioerosion have and will continue to occur as the tropical oceans become more acidified over the next few decades (e.g., Chan & Connolly, 2013; Pandolfi et al., 2011).

Nevertheless, while measurable OA of the tropical ocean has been underway for several decades now, detection and attribution of the effects of OA on reef-building corals have been challenging. Century-long records of coral calcification rates generated from skeletal cores do not show a consistent decline in calcification rates as ocean pH decreased through the 20th century. Rather, in some locations, coral calcification rates sharply decreased, others remained stable, and yet others increased over this time period (e.g., Cooper et al., 2008, 2012; De'ath et al., 2009; D'Olivo et al., 2013). Even where declines in calcification have been observed, our ability to attribute such changes to OA is confounded by the fact that ocean warming, sea level rise, changes in surface ocean productivity, and many localized anthropogenic disturbances are co-occurring with OA and also influence coral growth (e.g., Cooper et al., 2008; De'ath et al., 2009; Lough & Cantin, 2014; Pandolfi, 2015).

Massive long-lived *Porites* colonies are common on reefs across the Indo-Pacific, and their growth histories span the time period over which OA has occurred, providing a unique continuous archive of such impacts. The skeletal growth of *Porites* corals occurs in two steps in which the corals initially extend existing skeletal elements to enable upward growth, that is, extension, followed by thickening of those elements, that is, densification (Barnes & Lough, 1993). Extension, which is driven primarily by the creation of calcification "centers" or nucleation sites, is under strong biological control (presumably through the organic matrix) and less sensitive to OA (e.g., Cohen & McConnaughey, 2003; Crook et al., 2013; Fantazzini et al., 2015; Mollica et al., 2018; Nothdurft & Webb, 2007; Tambutte et al., 2015). In contrast, densification, which contributes the bulk of the skeletal mass and serves to reinforce the skeleton against the force of the waves and currents, is strongly sensitive to OA because crystal formation during this phase is under strong physicochemical control (e.g., Crook et al., 2013; Fantazzini et al., 2015; Martinez et al., 2019; Mollica et al., 2018; Rippe et al., 2018; Tambutte et al., 2015). Here we compile existing and new skeletal growth records of 95 *Porites* corals from the Great Barrier Reef (GBR) (De'ath et al., 2009), South China Sea (SCS) (Su et al., 2016), and the central Pacific Ocean (CPO) spanning the time period of 1871 to 2014 (section 2; Figure S1 in the supporting information) and use a coral skeletal growth model to isolate the effects of different factors and quantify their respective contributions to the coral growth, particularly to coral skeletal density.

2. Methods

2.1. *Porites* Skeletal Growth Parameters
2.1.1. GBR and SCS (Hainan Island) Reefs

Our analysis employs the annual *Porites* skeletal growth parameters (i.e., extension, density, and calcification) reported in previous studies of the GBR (De'ath et al., 2009) and the SCS (Hainan Island) reefs (Su et al., 2016). For the GBR, an updated version of the skeletal growth parameters originally reported in De'ath et al. (2009) is adopted, which excludes the incomplete outmost growth layers (De'ath et al., 2013). Although some other studies also reported *Porites* skeletal growth parameters on the GBR (e.g., D'Olivo et al., 2013), those data are not available in online repositories and are thus not included in our analysis. To robustly investigate the multidecadal variations in *Porites* skeletal growth, we focus on the time periods when at least 10 skeletal cores are available for each year and include only cores that have at least 50 years of growth within these selected time periods. Furthermore, we exclude the time periods when independent constraints of environmental parameters (e.g., temperature; Rayner et al., 2003) are not available. Together, these selection criteria result in the inclusion of 60 *Porites* cores from 39 reefs over the period of 1871–2000 for the GBR and 16 *Porites* cores from two reefs over the period of 1901–2000 for the Hainan Island, SCS (Figure S1). For each core, we calculate the percentage changes in its annual extension, density and calcification relative to the corresponding mean values over 1951–1960, a common period that all cores cover (Figure S2 and Data Set S1): $x_{i, rel} = \left(x_i / \overline{x_{i, c}} - 1 \right) \times 100$, where x_i is the skeletal growth parameter at a given year i and $\overline{x_{i, c}}$ is the mean value of that parameter over the common period for the same core.

2.1.2. CPO Reefs

Porites skeletal cores were collected from seven central Pacific reefs (Jarvis and Kingman in the Pacific Remote Islands Marine National Monument; Kanton, Nikumaroro and Rawaki in the Phoenix Islands Marine Protected Area; Kiritimati and Tutuila) and were imaged with a Siemens Volume Zoom Spiral Computerized Tomography scanner. Annual extension rates, skeletal densities, and calcification rates were then determined based on these CT images along polyp growth axes (Data Set S2, DeCarlo et al., 2015; Mollica et al., 2018). Similar to the GBR and SCS reef cores, we focus on the time periods when at least 10
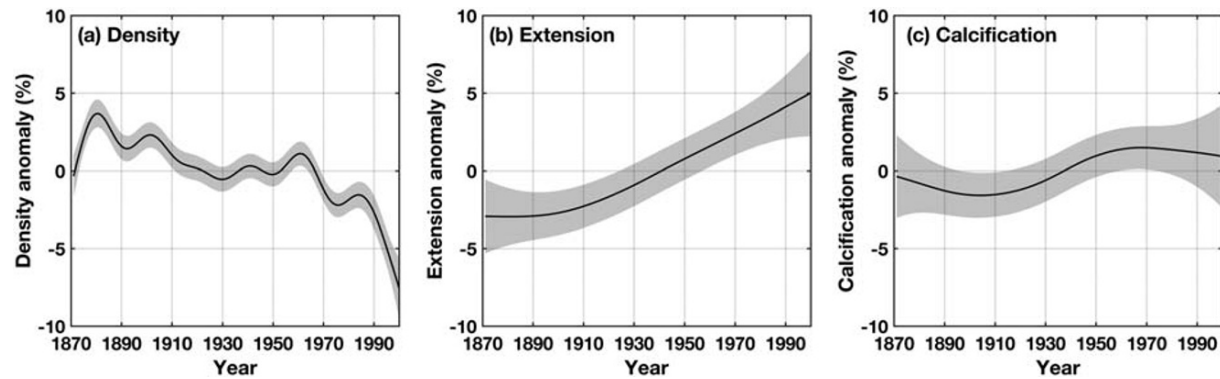
Figure 1. Partial-effects plots showing changes in *Porites* skeletal parameters at the Great Barrier Reef from 1871 to 2000: (a) density, (b) extension, and (c) calcification. The temporal trends were derived from 60 long (≥50 years) *Porites* skeletal cores from 39 reefs across the Great Barrier Reef (Figure S1, section 2, Text S3; De'ath et al., 2009) and are expressed as the anomalies relative to the corresponding mean values over 1951–1960, a common period that all cores cover. The gray bands indicate 95% confidence intervals for the predicted value for any given year.

skeletal cores are available for each year and include only cores that have at least 10 years of growth within these selected time periods. These lead to the inclusion of 19 *Porites* cores over the period of 1978–2014 in our analysis (Figure S1). We then calculate, for each core, the percentage changes in its annual extension, density, and calcification relative to the corresponding mean values over 1998–2007, a common period that all the CPO coral cores cover (see above; Figure S2 and Data Set S1).

2.2. Predicting *Porites* Skeletal Density With a Skeletal Growth Model

For each of our selected *Porites* cores, we predict its annual skeletal densities based on a skeletal growth model (Mollica et al., 2018; Text S1) and use them to evaluate and isolate the effects of three main factors that influence *Porites* skeletal density, that is, extension, temperature, and seawater carbonate chemistry. This skeletal growth model, building on previous studies of *Porites* skeletal growth (Barnes & Lough, 1993; Taylor et al., 1993), explicitly simulates the two distinct phases of *Porites* skeletal growth (i. e., extension and densification) and has quantitatively reproduced the experimentally measured *Porites* skeletal densities from a variety of reef environments (Mollica et al., 2018).

For each core, model simulations were conducted under three different conditions: (1) extension as the only forcing, that is, keeping temperature and seawater carbonate chemistry constant; (2) temperature as the only forcing, that is, keeping extension and seawater carbonate chemistry constant; and (3) extension and temperature combined as the forcing, that is, keeping seawater carbonate chemistry constant. For the parameters which were kept constant during the model simulations, their values were set as the mean values over the common periods for each core, that is, 1951–1960 for the GBR and the SCS reef cores and 1998–2007 for the CPO reef cores.

For all the model simulations, experimentally measured extension, seawater temperatures from the Hadley Centre Sea Ice and Sea Surface Temperature (HadiSST) v1.1 data set (1° × 1°, Rayner et al., 2003), and seawater pH and DIC outputs from the Community Earth System Model Biogeochemical historical run (CESM-BGC, Hurrell et al., 2013) were used. HadiSST v1.1 data set, although relatively coarse in spatial resolution compared to some other temperature data sets (e.g., OISST; Banzon et al., 2016), covers the whole time period of our core records (i.e., from 1871 to 2014) and has been used extensively in previous reef studies (e.g., De'ath et al., 2009). Similarly, seawater pH and DIC outputs from the CESM-BGC historical run were adopted due to the lack of constraints on past seawater carbonate chemistry in most reefs; but since seawater pH and DIC were kept constant in all our model simulations (see above), their exact values have negligible effects on our results, which focus on the relative percentage changes in skeletal density (Mollica et al., 2018). Other parameters in the *Porites* skeletal growth model (e.g., corallite area and tissue thickness) were assumed to be constant over the growth of each coral and set as either the average values reported for *Porites* corals in the region or the optimized values derived from *Porites* corals from multiple tropical reefs (Table S1; Lough & Barnes, 2000; Mollica et al., 2018; Su et al., 2016). We then analyzed these model-predicted skeletal densities the same way as the experimentally measured densities and calculated, for each
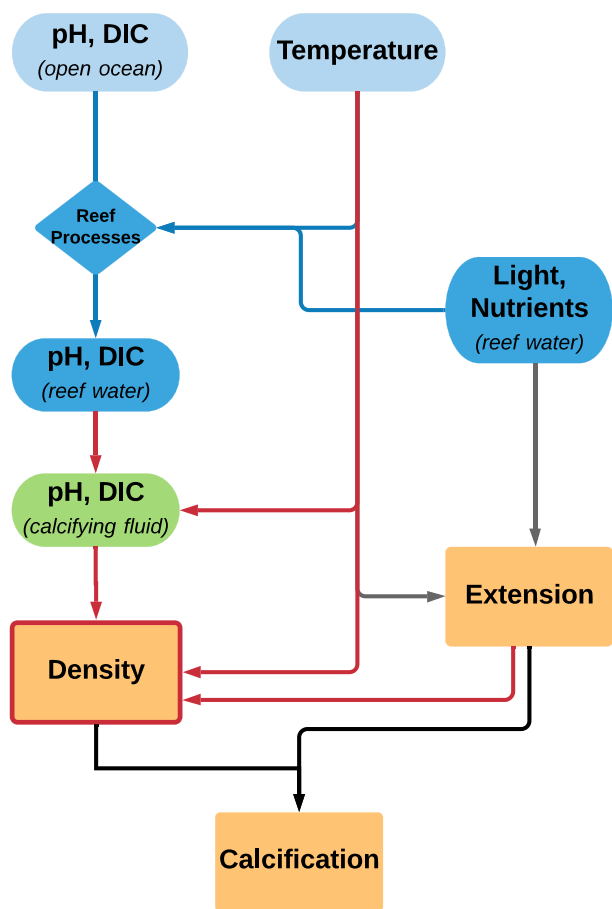
Figure 2. Relations between open ocean and reef water carbonate chemistry and their influences on *Porites* coral skeletal growth. *Porites* skeletal density is directly affected by the carbonate chemistry of its calcifying fluid, which in turn is influenced by reef-seawater chemistry (Guo, 2019; McCulloch et al., 2012, 2017; Mollica et al., 2018, Text S1). This makes *Porites* skeletal density most sensitive to ocean acidification. Besides seawater chemistry, *Porites* skeletal density is also directly affected by seawater temperature and the rate of skeletal extension (Mollica et al., 2018), while other environmental factors (e.g., light condition and nutrient levels) affect *Porites* skeletal density indirectly through their influences on the skeletal extension and/or reef-water chemistry. We use a coral skeletal growth model to isolate the effects of different factors and quantify their respective contributions to the coral growth (Equation 1; Figure 3). Arrows denote the processes that are explicitly (red) or implicitly (gray) simulated in our coral skeletal growth model, and the factors influencing reef water carbonate chemistry (blue).

core, the percentage changes in the model predicted annual densities relative to the corresponding mean of the common periods.

2.3. Constraints on the Reef-Water pH on the GBR

We compiled existing constraints on the reef-water pH on the GBR based on the boron isotope composition of coral skeletons at six GBR reef sites, including Arlington Reef, Flinders Reef, Pandora Reef, Havannah Island, Rib Reef, and Reef 17-065 (D'Olivo et al., 2015; Pelejero et al., 2005; Wei et al., 2009). To robustly investigate the multidecadal variations in reef-water pH at the GBR, we focused on the time periods when at least 5 pH records were available for each year. This limited our analysis to the period from 1966 to 2000 for the GBR (Figure S3; seven *Porites* cores in total). To remove the methodological inconsistency in pH estimations among different studies (e.g., regarding the use of boron isotope fractionation factors), we recalculated the seawater pH values based on the coral δ^{11}B data reported in each study using the same physicochemical parameters and method (Text S2 and Data Set S3; Dickson, 1990; D'Olivo et al., 2015; Foster et al., 2010; Klochko et al., 2006; Trotter et al., 2011). Then, for each $\delta^{11}B_{coral}$ record, we calculated changes in its estimated pH_{sw} relative to the corresponding mean over 1976–1985, a common period that all these records cover (Figure S3 and Data Set S3).

There are currently very limited constraints on the reef-water pH for the SCS and the CPO reefs (two for the SCS reefs; Liu et al., 2014; Wei et al., 2015; none for the CPO reefs), which precludes robust statistical analysis of the temporal trends in reef-water pH for these two regions.

2.4. Determining Temporal Trends in *Porites* Skeletal Growth Parameters and Reef-Water pH

We determined the temporal trends in (1) *Porites* skeletal growth parameters (both experimentally measured and model predicted) on the GBR, the SCS, and the CPO and (2) the reef-water pH records we compiled and recalculated for the GBR using the generalized additive mixed models (GAMMs). GAMMs are extensions to the generalized linear mixed models (GLMMs) and allow for nonlinear response (Wood, 2017). Similar methods have been used in previous studies of *Porites* skeletal growth (e.g., Cooper et al., 2012; De'ath et al., 2009, 2013; Ridd et al., 2013). In each model, year was set as the fixed effect component, while coral colony and reef site as the random effect components. A smoothing spline was applied to the fixed effect variable, with the degree of smoothness (i.e., the degrees of freedom associated with the smoothing function) determined through cross-validation (Cooper et al., 2012). All the models were analyzed using the *lme4* and *mgcv* packages in the R programming software with the REML method (Bates et al., 2015; Wood, 2011).

3. Results and Discussion

Temporal trends in skeletal growth parameters, determined using GAMMs (section 2; Wood, 2017), show that *Porites* skeletal density has decreased by ~11% on the GBR from 1871 to 2000 (Figure 1). This density decline is most significant between 1980 and 2000, reaching ~3% per decade, compared to ~0.5% per decade from 1871 to 1980. Declines in skeletal density are also evident in *Porites* colonies in the SCS and in the CPO, ranging from ~20% over 1901–2000 to ~7% over 1978–2014, respectively (Figure S4).

These density declines, although consistent with the negative impacts expected from OA, cannot be attributed exclusively to OA, because factors including skeletal extension (E) and seawater temperature (T) also influence coral skeletal density (Figure 2). Specifically, as extension increases, density will decrease, even
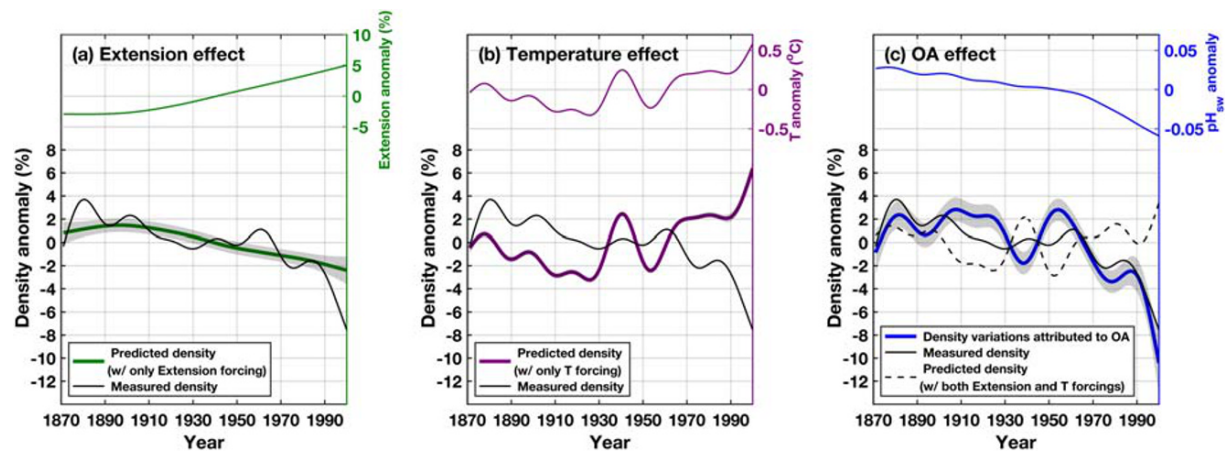
Figure 3. Contributions of different factors to the changes in *Porites* skeletal density at the Great Barrier Reef: (a) extension, (b) temperature, and (c) ocean acidification. The impact of ocean acidification is determined by subtracting the model predicted effects of extension and temperature (dashed line, panel c) from the measured density (black line; Equation 1). Also shown for comparison are the temporal changes in each factor (upper panels). All anomalies are calculated relative to the corresponding mean values over 1951–1960, a common period that all cores cover, and the seawater temperature and pH are derived from the HadiSST data set and the CESM-BGC historical run, respectively (section 2). The model-predicted high-frequency density variability around 1940 (b and c) likely arises from the uncertainties in the historical temperature data-products during this time period (see text for details).

if ocean pH does not change, because the less time a skeletal element resides within the coral tissue layer (i.e., at higher extension rate), the less it can be thickened and vice versa (Barnes & Lough, 1993; Mollica et al., 2018; Taylor et al., 1993). Conversely, skeletal density is expected to increase as seawater temperature increases, because calcium carbonate precipitates faster at higher temperatures (Burton & Walter, 1987; Mollica et al., 2018). Note that other environmental factors such as nutrients and water quality can also affect coral growth through their influences on extension (e.g., Al-Rousan, 2012; Dustan, 1975; Huston, 1985; Lough & Cooper, 2011; Tomascik & Sander, 1985) and are thus implicitly included in our analysis as well (Figure 2).

Indeed, at all three study sites, the density declines observed in the *Porites* corals over time were accompanied by increases in skeletal extension, ranging from ~9% at the GBR to ~30% in the SCS and by temperature variations up to 1.5°C (Figures 1, 3, S4, and S5). We estimated the contribution of these extension and temperature changes to the observed density declines using a skeletal growth model that explicitly simulates the two-step skeletal growth of *Porites* corals and links the coral calcifying fluid chemistry with external seawater conditions (section 2; Mollica et al., 2018). The model predicts that skeletal extension acting alone would have caused a modest decline in skeletal density of ~4% on the GBR over the time period from 1871 to 2000 (Figure 3a). Conversely, variations in water temperature alone, especially the increase post-1950, would have caused an ~6% increase in skeletal density over the same time period (Figure 3b). Together, skeletal extension and ocean warming are expected to lead to oscillations of *Porites* skeletal density between −2% and 2% during 1871–2000, not the decrease in density as observed (Figure 3c).

OA, skeletal extension, and temperature are the main influences of the skeletal density of *Porites* corals (Figure 2; Mollica et al., 2018). Previous model simulations, explicitly considering these three factors, have quantitatively reproduced the experimentally measured *Porites* skeletal densities from a variety of reef environments (Mollica et al., 2018). Thus, having constrained the effects of temperature and extension, we can assess the impact of OA on *Porites* density (ΔD_{OA}) by subtracting the model predicted density changes induced by extension and temperature variations ($\Delta D_{E+T,modeled}$) from the measured density changes ($\Delta D_{measured}$):

$$\Delta D_{OA} = \Delta D_{measured} - \Delta D_{E+T,modeled} \qquad (1)$$

Figure 3c shows the OA-driven changes in the skeletal density of *Porites* corals on the GBR since 1871. OA-driven changes are small, fluctuating between 2% and −2%, until 1950, after which a rapid ~13 ± 3% (95% confidence interval) decline in density is observed from 1950 to 2000. The timing of the OA effect is consistent with the accelerated decline in the ocean pH post-1950. However, the magnitude
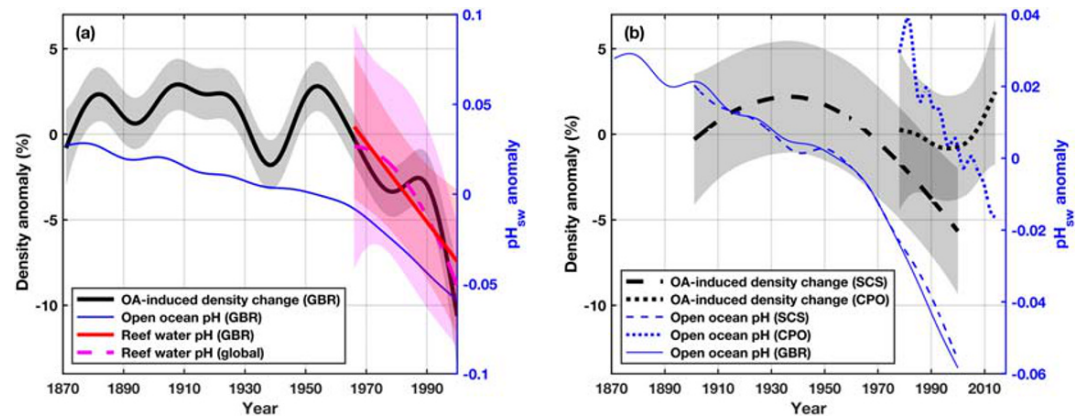
Figure 4. Impacts of OA on *Porites* skeletal density at different reef systems and their correlations with ocean and reef-water pH: (a) Great Barrier Reef (GBR); (b) South China Sea (SCS) and central Pacific ocean (CPO) reefs. The declines in reef-water pH at the GBR (section 2; D'Olivo et al., 2015; Pelejero et al., 2005; Wei et al., 2009) and other reefs around the globe (Cyronak et al., 2014) are shown in panel (a). Also shown for comparison are the open-ocean pH derived from the Community Earth System Model Biogeochemical (CESM-BGC) historical run. The gray and colored bands indicate 95% confidence intervals.

of the ocean pH decrease post-1950 is too small to explain the dramatic decline in skeletal density on the GBR. In fact, the skeletal growth model predicts a density change of ~1% given a 0.06 change in seawater pH alone.

This discrepancy is explained by the enhanced acidification of reef-water on the GBR relative to the open ocean (Figure 4a, section 2; D'Olivo et al., 2015; Pelejero et al., 2005; Wei et al., 2009). In particular, boron isotope analysis of *Porites* skeleton shows that reef-water pH on the Arlington Reef (midshelf, northern GBR) has decreased by ~0.2 unit since the 1940s (section 2; Wei et al., 2009), which is about 2.5-fold larger than the decrease in open ocean pH over the same time period (i.e., ~0.06 unit). This enhanced acidification of reef-water has also been observed at inshore reefs in the GBR and at other coral reefs around the globe, where reef-water pCO_2 has increased 2.5–3.5-fold faster than the open ocean over the past 20–30 years, potentially as a result of increased inputs of terrestrial nutrient and organic matter (Figure 4a; Cyronak et al., 2014; Uthicke et al., 2014).

Our model does predict some high-frequency density variability that is not replicated in the measured data, especially around 1940. This variability is driven by the temperature input to the model. It is likely that well-documented uncertainties in the historical temperature data products during this time period (e.g., Chelton & Risien, 2016) confound our estimation of the temperature effects on *Porites* density and caused the ~4% decline in density around 1940 that we currently attribute to OA. Efforts to increase the accuracy of the historical temperature records (e.g., Chan et al., 2019) will improve our estimates of the OA impact on coral skeletal growth. Overall, however, the model-predicted effects of extension and temperature on skeletal density are in good agreement with the independently measured density changes (Figures 3a and 3b), and our results indicate strong impacts of OA on GBR corals post-1950.

Analysis of *Porites* growth records from Hainan Island, SCS indicate that here too, OA has caused ~7 ± 3% (95% confidence interval) decline in *Porites* skeletal density from 1901 to 2000, with the most significant decline also starting around 1950 (Figures 4b and S5 and Text S4). The similar timing of the estimated OA impacts on the GBR and the SCS corals occurs despite the dramatically different bulk skeletal growth records at these two regions (Figure S4) and is consistent with the similar evolution of ocean pH around the GBR and the SCS (Figure 4b). In contrast, analysis of CPO reef corals suggests that OA has not yet had a significant influence on *Porites* growth in the region (Figures 4b and S5 and Text S4). This is likely because these reefs are bathed in open-ocean seawaters and have thus experienced relatively modest decreases in their reef-water pH to date.

Our study presents strong evidence that 20th century OA, exacerbated by reef biogeochemical processes, has had measurable effects on the growth of a key reef-building coral across the GBR and in the SCS. These

effects will likely accelerate as OA progresses over the next several decades. While it is difficult to directly extrapolate our estimated OA impact to any specific reef due to the variability of reef-water pH among and within different reefs (e.g., D'Olivo et al., 2015; Gagliano et al., 2010; Mongin et al., 2016; Uthicke et al., 2014), we expect broadly similar magnitudes of OA impact worldwide because enhanced acidification of reef water pH similar to the GBR has been observed in many coral reefs around the globe (Figure 4a, Cyronak et al., 2014).

Declines in coral skeletal density increase the susceptibility of coral skeletons to bioerosion, dissolution, and storm damage (e.g., Crook et al., 2013; DeCarlo et al., 2015; Fantazzini et al., 2015; Madin et al., 2012; Wisshak et al., 2012) and suggest structurally weaker and more vulnerable coral reefs in the 21st century. In particular, the strength of coral skeleton decreases exponentially with decreasing skeletal density, for example, about 60% reduction of compressive strength for a 13% density decline (Chamberlain, 1978; Madin, 2004; Madin et al., 2008; Scott & Risk, 1988), making the coral skeletons increasingly susceptible to storm damage. This, together with the deleterious influences of other global and local environmental stressors (e.g., ocean warming, sea level rise, and pollution), poses severe challenges for the health and survival of coral reef ecosystems and their exceptional biodiversity. Better understanding of the controls on the reef-water pH and coral calcification mechanisms will enable more accurate projections of OA impacts on coral reef ecosystems and thus the developments of potential mitigation strategies.

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